

MATHEMATISCHES FORSCHUNGSINSTITUT OBERWOLFACH

Tagungsbericht 23/1975

Mathematische Modelle in der Biologie

1.6. bis 7.6.1975

Die Tagung über "Mathematische Modelle in der Biologie" stand unter der Leitung von K. P. Hadeler (Tübingen), W. Jäger (Heidelberg) und H. Werner (Münster). Das Ziel dieser Tagung war, eine Übersicht über die Anwendung mathematischer Methoden bei biologischen Problemen zu gewinnen. Hierbei standen die Analysis und die Topologie im Vordergrund, doch war auch die Stochastik mit Teilgebieten vertreten. Die behandelten Gegenstände lassen sich wie folgt gruppieren: 1. Lineare Diffusionsgleichungen in Zusammenhang mit Modellen für die Nervenleitung, Ausbreitungsphänomene in der Genetik, in der Oekologie, und in der Theorie chemischer Reaktionen, 2. Modelle für die Entstehung von Strukturen, 3. Modelle aus der Epidemiologie und Immunologie, 4. Optische Perzeption.

Aus mathematischer Sicht bestehen zwischen den genannten Punkten jeweils engere Verbindungen. In der Stochastik lag der Schwerpunkt auf den Verzweigungsprozessen. Die topologischen Methoden wurden in zwei Übersichtsvorträgen dargestellt.

Einige Vorträge zeigten, daß auch andere Gebiete der Mathematik (Algebra, Gruppentheorie) zu Lösungen für biologische Probleme führen können. Hier gibt es noch ein weites Feld für mathematische Anwendungen.

Die Kommunikation zwischen den Arbeitsrichtungen war gut, allerdings zeigten die Erfahrungen dieser Tagung, daß es wünschenswert ist, noch nähere Verbindung zu experimentell arbeitenden Biologen und Medizinerinnen zu suchen.

Die Tagung ergab, daß das Gebiet in Deutschland, abgesehen von einigen wenigen Schwerpunkten, kaum entwickelt ist. Dagegen hat die Beschäftigung mit der Biologie im Ausland, vor allem in den USA, viele Mathematiker aus verschiedenen Gebieten, insbesondere der Analysis, angezogen.

Die nachhaltige Unterstützung durch die Institutsleitung, die diese Tagung ermöglicht hat, wird dankbar anerkannt.

Teilnehmer

W. Alt, Münster	P. de Mottoni, Rom
J. Batt, München	I. Nasell, Stockholm
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B.D. Coleman, Pittsburgh	R. Regges, Aachen
Ch. Conley, Madison	G.H. Renninger, Guelph
K. Dietz, Genf	H.L. Resnikoff, Münster
L. Edler, Mainz	F. Rothe, Tübingen
J.W. Evans, La Jolla	L.A. Segel, Rehovot
P.C. Fife, Tucson	B.D. Sleeman, Dundee
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U. an der Heiden, Tübingen	D. Steinhausen, Münster
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W. Jäger, Heidelberg	R. Thom, Bures-sur-Yvette
K. Jänich, Regensburg	W. Vogel, Bonn
N. Kaplan, Kopenhagen	H.-O. Walther, München
R. Keller, Regensburg	P. Waltman, Iowa City
L. Lander, Regensburg	H. Werner, Münster
D. Ludwig, Vancouver	A. Wörz, Tübingen
H. Maurer, Köln	E.C. Zeeman, Coventry
H. Meinhardt, Tübingen	R. Zielke, Tübingen
B. Mellein, Mainz	B. Zwahlen, Lausanne

Vortragsauszüge

J.E.COHEN: An ergodic theorem for the age structure of large populations in markovian environments

The ergodic theorems of demography show that the present age structure of a unisexual, closed population is independent of the population's age structure in the sufficiently remote past, but depends entirely on the recent history of vital rates (birth and death rates). The ergodic theorem presented here supposes that at each instant in discrete time, the array of age-specific birth and death rates to which a unisexual closed population is subject is drawn from a set S of such arrays. Given two initial populations, and two initial arrays of vital rates from S, the vital rates in the next instant of time are chosen from S according to a Markov chain of a certain kind, independently for each of the two populations. Then all moments of the age structures of the two populations converge and the age structures converge in distribution.

J.E. Cohen, Ergodicity of Age Structure in Pop. with Markovian Vital Rates. I. Countable States. J. of the Am.Stat.Ass. 1976.
W. Brass, Perspectives in Population Prediction. J. of the Roy. Stat. Soc. Series A 137(4), 532-583, 1974.

B.D. COLEMAN: On periodic solutions of some unusual non-linear integral equations with applications in neurobiology

Solutions r of the equation \

$$r(t) = m(e(t) - \frac{A}{\delta} \int_0^{\infty} e^{-s/\delta} r(t-\tau-s) ds) \quad , \quad (1)$$

with A , τ , and δ positive constants and m the "positive part" function defined by $m(x) = \frac{1}{2}(x + |x|)$, appear to give a good description of the response of certain retinae, including that of the compound eye of Limulus, to spatially uniform excitations $e(t)$. George H. Renninger and I have recently shown that if A and τ/δ are in appropriate ranges, then, for e held constant,

(1) has a non-constant periodic solution which can be written in closed form in terms of elementary functions. This solution shows a sustained synchronous "bursting phenomenon" in which the time-intervals of neural activity in the optic nerve alternate with rest periods. Possible physiological uses of such oscillations will be discussed, and recent analytical results on a generalization of (1) will be presented.

B.D.Coleman, Rendiconti dell'Istituto Lombardo A (1975)(in press), B.D.Coleman, SIAM J. o.Appl.Math.(1975)(in press).

CH.CONLEY: Travelling waves

This report concerns the existence and stability of travelling wave solutions of the equation $u_t = Du_{xx} + f(u, \epsilon)$ where t and x are scalars, $u(t, x)$ is an n -vector, D is a diagonal matrix of (positive) diffusion constants and ϵ is a positive parameter.

The first step is to construct travelling waves for small ϵ making use of properties of the (singular) limiting case when ϵ is zero. Ideas from the qualitative theory of ordinary differential equations play the main role here. The second step is to try to analyze ("linearized") stability of the travelling solution of the P.D.E. This again comes down to the study of an ordinary differential equation. Some partial results are described for equations of the type of the Hodgkin-Huxley equations.

G.A. Carpenter, "On travelling wave solutions of the Hodgkin-Huxley equation"; Thesis, University of Wisconsin 1974. C.Conley, "On travelling wave solutions of non-linear diffusion equations". M.R.C. Tech. Summary Report No. 1492. C.Conley, R.Easton, "Isolated invariant sets and isolating blocks", T.A.M.S. Vol.158, No.1, July 1971, pp. 35-61. C.Conley, "On the continuation of invariant sets of a flow", Actes, Congrès intern. Math. 1970. Tome 2, p.909-913. S.Hastings, "The existence of periodic solutions to Nagumo's equation", Quart.Journ.of Math.1974.

K.DIETZ: Models for the pair formation of parasites

Male and female parasites are assumed to enter the host according to independent Poisson processes with constant rates λ . They die at a constant rate μ . They form immediately pairs if a

parasite of the opposite sex is available. They do not remate after the death of one partner. The death rate of a pair is ν . Then the expected number of pairs tends to the limit value

$$\frac{\lambda}{\nu} \left\{ 1 - \left[1 + 2 \frac{g}{1+g} {}_1F_1(1; g+2; g) \right]^{-1} \right\}$$

where $g = \lambda/\mu$. In order to approximate the transient behavior of the number of pairs for large and small μ , two simplified models are considered. (K. Dietz, Theor. Pop. Biol. 8, 1975).

L. EDLER: A general age dependent branching process with variable life time and generation time distribution

A general age dependent branching process with generation dependent life time and generation time distribution describes the development in time of a population, where each individual I has a random life time L_I and produces during his life at random ages (called generation times) $T_I^{(1)} \leq T_I^{(2)} \leq \dots \leq L_I$ one offspring, who belongs to the next generation and behaves in the same fashion. The behavior of each individual is independent of all others (branching property). The probability distribution of $(L_I, T_I^{(\nu)})$, $\nu=1,2,\dots$ may depend on the generation I belongs to. This branching process generalizes those of CRUMP-MODE. J. Math. An. Appl. 24,25 and FILDES, Adv. Appl. Prob. 4,6.

Let $Z_i(t)$ be the number of individuals alive at time t , the initial individual born into the i -th generation. Integral equations are derived for the moments of $Z_i(t)$ and under several conditions there is a constant b_i such that $Z_i(t)/b_i E Z_i(t)$ converges in mean square to a random variable W_i , $i=0,1,\dots$.

J.W. EVANS: Nerve impulse stability

Let $V_t = \begin{pmatrix} v^0 \\ 0 \\ \vdots \\ 0 \end{pmatrix} + f(V)$ be a set of axon equations with a

resting state at $V=0$. If the system is exponentially stable at rest than there is a function $\phi(v,y)$ which for a fixed $v > 0$ is the unique candidate for the nerve impulse arising from zero at ∞ . If $\phi(v_0,y) \rightarrow 0$ as $y \rightarrow -\infty$ then the stability properties of $\phi(v_0, \cdot)$ viewed in the $y=x-v_0 t$ coordinate system are given by the zeros of an analytic function $D(\lambda)$ which determines the eigen-

values of the generator of the linearized system of equations about $\phi(v_0, \cdot)$. The sign of $(\partial D/\partial \lambda)(0)$ plays a critical role in the behavior of $(\partial \phi/\partial v)(v, y)$ as v increases through v_0 for large negative y .

Nerve axon equations I, II, III & IV; Indiana Univ. math. J. Vol. 21 no 9, March 1972, 877-885 Vol. 22, no 6, December 1972, 577-593 and Vol. 22 no 1, July 1972, 75-90 and to appear.

P.C.FIFE: Pattern formation in reacting and diffusing systems

The question of the genesis of spatial order in biological systems is approached by investigating the spontaneous appearance of order in reacting and diffusing systems. A mechanism is described, whereby stable sharply differentiated (dissipative) structures can evolve naturally within a mixture of reacting and diffusing substances. The model has two reacting components, with one diffusion coefficient much smaller than the other. Unlike patterned states obtained by small amplitude analysis near uniform states, our structures have large amplitude and serve to divide the reactor into subregions, each corresponding to a distinct phase for the system. A singular perturbation analysis and the theory of the motion of wave fronts is used to deduce the evolution of such states from arbitrary initial data.

K.P.HADELER: Wave fronts in Fisher's model and related problems

Consider a system $\dot{u} = f(u, v, c)$, $\dot{v} = g(u, v, c)$, c a real parameter, in a domain of \mathbb{R}^2 . Assume the only stationary points are a saddle at s_1 and another point s_2 , which is a stable vortex for $c < c^*$, a stable node for $c > c^*$. A trajectory leaving s_1 with the unstable manifold and arriving at s_2 with defined direction is called a front. The corresponding value of the parameter c is called speed. We give sufficient conditions for the existence of fronts, in particular conditions for a closed upper half-line of fronts. The results can be applied to nonlinear diffusion equations and epidemic models. The speeds in Fisher's model can be explicitly determined for all cases of interest.

K.P.Hadeler, F.Rothe: Travelling fronts in nonlinear diffusion equations, J.o.Math.Biol.1975.

U. AN DER HEIDEN: Ober ein kontinuierliches Nervenmodell

Die Funktionaldifferentialgleichung

$$\frac{1}{a} \dot{x} + x = \frac{1}{1 + \exp \left\{ -f + b \int_0^{\infty} x(t-u) [e^{-pu} - e^{-qu}] du \right\}}$$

ist ein Modell für den zeitlichen Verlauf der normierten Impulsfrequenz $x(t)$ eines Neurons in Abhängigkeit vom Input $f(t)$. Sie läßt sich in ein nichtlineares System dritter Ordnung gewöhnlicher Differentialgleichungen überführen. Ist dessen stationäre Lösung instabil, so existieren periodische Lösungen bei konstantem Input. Ist f ω -periodisch, so gibt es eine ω -periodische Lösung, die, für den Fall, daß $b(q-p) < 16 pq$, global asymptotisch stabil ist.

Jedes aus Neuronen dieser Art gebildete Nervennetz hat zu jedem konstanten Input einen stationären Zustand. Dieser ist eindeutig und stabil, wenn die Eigenwerte der Matrix aus den Verknüpfungskoeffizienten gewisse Bedingungen erfüllen.

U. an der Heiden, Existence of periodic solutions of a nerve equation, Biological Cybernetics (to appear).

F.C. HOPPENSTEADT: Population waves

The phenomenon of waves occurring in a population's birth rate will be described. This begins with a description of Bernardelli waves arising in the linear renewal theory. Then a modification is introduced which involves a density dependent fertility; thus, a nonlinear renewal equation must be analyzed. A discrete version of this is analyzed: It is shown that there are multiple bifurcations of periodic solutions with eventual transition to chaos, i.e., the appearance of an infinity of periodic solutions. The dynamics are described in the chaotic regime by means of numerically determined density functions for solutions.

F.Hoppensteadt, Mathematical theories of populations: Demographics, genetics and epidemics, SIAM Publications, Philadelphia, 1975.

F. Hoppenstaedt and J.M.Hyman, The transition to chaos of solutions to a logistic difference equation (in press).

N.KAPLAN: A branching process with disasters

A population process is considered where particles reproduce according to an age-dependent branching process, and are subjected to disasters which occur at the epochs of an independent renewal process. Each particle alive at the time of a disaster, survives it with probability p and the survival of any particle is assumed independent of the survival of any other particle. Necessary and sufficient conditions are given for almost sure extinction. In the case when extinction is not sure, the asymptotic growth is determined.

N.Kaplan, Sudbury, A., Nelsen, T.; A branching process with disasters. J. of Appl. Prob. March 1975. Athreya, Kaplan, Limit theorems for a branching process with disasters, preprint no.8, 1975- Instit. of Math. Stat., Univ. of Copenhagen.

D.LUDWIG: Persistence of dynamical systems in the presence of noise

Random perturbation may decisively affect the long term behavior of dynamical systems. The deterministic concept of stability no longer applies. It can be replaced by the expected time elapsed before leaving a domain of attraction. The expected time elapsed is computed by means of an asymptotic solution of a diffusion equation, for small noise. This theory can be applied to problems in population biology.

D. Ludwig, Persistence of dynamical systems under random perturbations, to appear in SIAM Review (1975). A.D.Ventzel and M.I. Freidlin (1970), On small random perturbations of dynamical systems. Uspekhi Math. Nauk, 25, pp.3-55. G.F.Miller (1962) The evaluation of eigenvalues of a differential equation arising in a problem in genetics, Proc. Camb. Phil. Soc. 58, 588-593.

H.MAURER: Einige Anwendungen der Theorie optimaler Steuerprozesse in der Ökologie

Erst in den letzten Jahren sind Anwendungen der Theorie optimaler Steuerprozesse auf Biologie und Ökologie untersucht worden. Die Schwierigkeit bei ökologischen Prozessen liegt im Gegensatz zu physikalischen und technischen Prozessen darin, geeignete dynamische Modelle zu formulieren. In diesem Vortrag werden zwei einfache Modelle als Steuerungsprobleme behandelt. Zunächst wird

ein gesteuertes Räuber-Beute-Modell nach B.S. Goh et al. betrachtet, das auf dem Volterra-Lotka-Modell basiert. Die Steuerung erfolgt dabei durch ein Insektizid, welches die Beute (Pest) oder die Räuber bzw. Beute und Räuber tötet. Im zweiten Modell wird ein logistisches Modell für das Wachstum der Population angenommen und damit das Problem des "optimalen Fischens" nach C.Clark diskutiert. Bei einer Fischart ist die Lösung vollständig bekannt, das Problem zweier Spezies jedoch ist nur teilweise gelöst und es werden Lösungsansätze skizziert.

B.S.Goh, G.Leitmann, T.L. Vincent: Optimal control of a prey-predator system, Math. Biosc. 19, 263-286 (1974). C.W.Clark, The economics of overexploitation, Science 181, 630-634 (August 1973). C.W. Clark, Mathematical problems in biological conservation, Report, Dept. of Math., Univ. of British Columbia, Vancouver, Canada 1973. H.T. Banks, Modeling of control and dynamical systems in the life sciences, in "Optimal Control and its Application", Part I, Lecture Notes in Economics and Math. Systems, Vol. 105, Springer Verlag, 1974.

H.MEINHARDT: Formation of netlike structures during morphogenesis

During the development of an organism, very complicated netlike structures such as blood vessels and leaf veins are made. A possible mechanism for generating such structures could be the following: By interaction of two substances, the activator and the inhibitor, a local high activator concentration is generated. This is used as a signal for a small group of cells to differentiate. If a stripe is to form, the next cell to differentiate should be that neighbor of the already differentiated cell, the sum of whose is maximum from these cells. This can be achieved through the agency of a third substance, which is produced everywhere and consumed or transported away by the differentiated cells. The production of the activator must be dependent on this "driver"-substance. The system is described by four partial differential equations. Numerical calculations show the formation of the desired netlike structure. - The mechanism of activator-inhibitor interaction can be found in: Gierer & Meinhardt, Kybernetik Dezember 1972, Applications to biological problems in Journ. of Cell Science 15 (74) 321.

P. DE MOTTONI: Stability problems for a system of reaction-diffusion equations

We consider a system of nonlinear equations of diffusive type, together with vanishing Dirichlet condition and (positive) Cauchy data. We ask about existence and stability of (positive) stationary solutions. It turns out that the stationary solutions of the system are characterized by the stationary solutions of a single non-linear elliptic equation. Then conditions for the existence of a non-trivial solution are easily given. As to the stability, for the trivial solution we make use of Lyapunov's general criterion, whereas for the nontrivial solution the same method, although in principle applicable, is not of practical use. We then prove the system to be equivalent - in view of its peculiar structure - to a single integro-differential equation, for which we construct a monotone iteration procedure, which provides an Einschließungssatz and hence an a priori bound for the whole system.

D. Sattinger, Topics in stability and bifurcation theory, Lect. Notes in Math., Springer, Berlin 1973. P. de Mottoni, A. Tesei, in Applicazioni del Calcolo, Scritti offerti a Mauro Picone in occasione del suo 90. compleanno, Veschi: Roma 1975.

I. NÄSELL: A mathematical model of Schistosomiasis with snail latency

Schistosomiasis is a serious tropical parasitic infection. One phase of the life cycle of the causative parasite is spent in human beings, and another phase is spent in certain species of fresh water snails. A hybrid model (i.e. a model with both stochastic and deterministic ingredients) is established for the transmission of Schistosomiasis in a community. The model allows for latency and differential mortality in the snail population. An important threshold behavior is predicted on the basis of properties of the solution of a system of nonlinear differential equations. Conditions under which the infection will be eradicated are studied. The efficiencies of various methods of control or eradication are investigated.

I. Näsell & W.M. Hirsch, The transmission dynamics of Schistosomiasis,

Communications on Pure and Applied Mathematics, 26(1973), 395-453. I. Näsell, A mathematical model of Schistosomiasis with snail latency, Trita-Mat-1975-2, Dept. of Math., Royal Inst. of Technology, Stockholm (1975).

T.POGGIO: The visual system of the fly: An example of a functional description of nonlinear (nervous) interactions

An approximative description of a class of many inputs, non-linear, interactive networks is introduced through the Volterra series formalism. In this way a kind of canonical classification of nonlinear interactions provides a conceptualization of the relevant information processing performed by a network. The "computational" properties of "Volterra networks" can be further characterized through an interesting connection with a theory of Analog Perceptrons.

The Volterra formalism is applied to behavioural studies of the part of the nervous system of the fly which underlies visual orientation and pattern discrimination. Antisymmetric, second order interactions between pairs of inputs are responsible for direction sensitive movement detection. Excitatory, single channels (weighted according to their location in the eye) probably provide the position dependent information responsible for the fly's orientation towards small objects. Surrounding nonlinear, fourth order inhibitory interactions affect selectively the "attractiveness" of more structured patterns. The interplay between nonlinear excitation and inhibition in this nervous network underlies simple cases of figure-ground extraction and is probably critically important for spontaneous pattern discrimination.

Poggio, Reichardt, A theory of the pattern induced flight orientation of the fly *Musca*, I, 12, 185-203 (1973) *Kybernetik*. Poggio, Reichardt, A theory of the pattern induced flight orientation ..., II, 18, 69-80 (1975), *Biol. Cybernetics*. Geiger, Poggio, The orientation of flies towards patterns: on the search for the underlying functional interactions, 19, (1975) *Biol. Cybernetics*. Poggio, Reichardt, Nonlinear interactions in the visual system of the fly, *Symp. on Quantitative Biology*, Cold Spring Harbor (1975) (in press)

T.POSTON: Zeeman's heartbeat & nerve impulse models

An account of Zeeman's paper "Differential equations for the heartbeat and nervous impulse" (in Towards a Theoretical Biology 4, Ed.C.H.Waddington, 1972, Aldine-Atherton, Chicago), with attention more on the mathematical motivation than on the resulting detailed models. In particular, discussion of whether a fast foliation /slow manifold structure is in fact logically necessary if a differential equation is to show "jump" behavior at a threshold; in what sense lemma 3 (the impossibility in R^2 of smooth return to equilibrium after such jumps) is true; and whether the nerve impulse equations of § 2.7 do correspond to a flow on the cusp surface, with jumps at folds:

R.REPGES: Application of prigogine's stability conditions in physiology

Some general methods are developed to derive mathematical equations for some class of physiological problems. It seems to be essential, that the linear relations between forces and fluxes must be replaced by nonlinear relationships, in order to get steady state conditions far from equilibrium and patterns in time (oscillatory) and space. The use of Prigogine's stability conditions for such cases is demonstrated.

Glansdorff, Prigogine, Structure, stability and fluctuations
Wiley 1971;

Katchalsky, Curvan, Nonequilibrium thermodynamics in Biophysics,
Harvard University Press, Cambridge Mass., 1964.

H.L.RESNIKOFF: On the psychophysical function

A psychophysical function $y=f(x)$ expresses the relationship between the magnitude x of a physical stimulus and the magnitude y of the sensory response evoked by that stimulus. G.T. Fechner proposed that $y = a_0 \log x$ if x denotes light intensity and y denotes perceived brightness. S.S.Stevens later proposed $y=c_0 \cdot x^{a_1}$ instead. Unfortunately, neither function agrees with experimental

data except on small subsets of the domain of f . Based upon several simple general principles for the phenomenological description of data, we propose the solution of

$\log \frac{dy}{dx} = a_0 + a_1 \log x + a_2 \log^2 x$ as the psychophysical function for brightness. If $a_2=0$, the solution is Stevens' function; if both $a_2=0$ and $a_1=0$, it is Fechner's function. The proposed function, which is the cumulated lognormal probability density, is in good agreement with observation. For classic data of Koenig and Brodhun, $a_0 = 3.833$, $a_1=0.137$, $a_2 = -0.024$ for x measured in millilamberts and y in just noticeable differences. Thus we find that the entire range of brightness perception of Brodhun's eye encompasses 643 just noticeable differences, a prime number.

To appear in J.Math.Bio.

F.ROTHE: Ober das asymptotische Verhalten der Lösungen einer nichtlinearen parabolischen Differentialgleichung

Die nichtlineare parabolische Differentialgleichung $p_t = p_{xx} + F(p)$ ist von R.A. Fisher als Modell zur Ausbreitung eines Gens vorgeschlagen worden. Man kennt wellenförmige Lösungen $\phi(x-ct)$ für gewisse Werte von c . Mit Hilfe von Lyapunovfunktionalen, die im wesentlichen Mittelwerte der Ausbreitungsgeschwindigkeit sind, wird gezeigt, daß die Lösungen obiger Differentialgleichung für gewisse Anfangsbedingungen im Limes großer Zeiten wellenförmig sind, wobei die asymptotische Wellengeschwindigkeit durch das Abklingverhalten der Anfangsbedingung für große x gegeben ist. F.Rothe, Dissertation Tübingen 1975.

L.A.SEGEL: Mathematical models for bacterial chemotaxis

Many bacteria can move through the action of one or more whip-like flagellae. Typically, such bacteria are chemotactic; i.e. they move preferentially toward or away from certain chemicals. Models on various levels for this phenomenon will be constructed and analyzed. Suitable limits of biased random walk models lead to sets of nonlinear partial differential equations. These same equations can be obtained phenomenologically. The formation and propagation of nonlinear travelling wave

solutions will be discussed. Recent extensions of the analysis will be treated, wherein the chemical interaction between receptor and signaling molecules is taken into account.

J. Mechanochemistry & Cell Motility 2, 25 (1973),

J.Th.Biol. 30, 235 (1971), J.Th.Biol. 46, 189 (1974), J. Th.

Biol. (1975), in press.

B.D.SLEEMAN: Nagumo's simplified model of nerve conduction

In this lecture we consider an initial boundary value problem for the system of evolutionary equations

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u)(u-a)-bv,$$

$$\frac{\partial v}{\partial t} = u, \quad 0 < a < 1, \quad b \geq 0,$$

$$x, t \in [0, \infty) \times (0, \infty).$$

After briefly describing the physiological interpretation of this system as a model governing the propagation of impulses in nerve axon we describe some of the recent results obtained in the case of travelling wave solutions.

The more difficult problem of studying the Nagumo system as an initial boundary value problem has received little investigation and in this lecture we endeavour to initiate such a study. In particular we consider questions of existence and uniqueness and demonstrate that a is essentially a threshold parameter. The asymptotic behavior and stability of solutions is also discussed.

Evans, J.W., Indiana Univ. Math. J. 21, 877-885 (1972), Ibid 22 75-90 (1972) Ibid 22 577-594 (1972). Green M.W., Sleeman B.D., J. Math. Biol. 1, 153-163 (1974). Levine H.A., Sleeman B.D., Battelle advanced studies center, Switzerland, Math. report no. 69 (1972)

H.THIEME: Diskussion eines Modells für die räumliche Ausbreitung einer Epidemie

Eine ansteckende Krankheit, die fortwährende Immunität gegen eine erneute Ansteckung hervorruft, breitet sich räumlich aus, indem die infektiösen Individuen Infektivität (z.B. in Form

von Bakterien) erzeugen, die sich durch Diffusion verbreitet und, in genügend hoher Dosis aufgenommen (siehe K.L.Cooke: 1967), die Erkrankung verursacht.

Für die Größe des suszeptiblen Bevölkerungsteils und dessen Endgröße werden Gleichungen hergeleitet und in Anschluß an Ideen D.G. Kendalls (1957 zu einem anderen Modell) der Begriff einer Pandemie mathematisch formuliert. Es ergeben sich Bedingungen für das Auftreten, bzw. Nichtauftreten von Pandemien, die an die Schrankentheoreme für Epidemien ohne räumliche Ausbreitung erinnern.

Bailey, N.T.J., The mathematical theory of epidemics, New York: Hafner 1957. Bartlett, M.S., Measles periodicity and community size. J.R. Stat. Soc., Ser.A, 120, 48-70 (1957).

R.THOM: Comparative embryology of Vertebrates and Arthropoda

We try to show that gastrulation in Arthropoda has an inverse interpretation of the one given for Vertebrates. The "prey" is realized by ectoderm in Vertebrates, by yolk in Arthropoda. Effects of this difference on neurulation are evaluated.

R.Thom, Structuralism and Biology, in "Towards a Theoretical Biology IV", C.H. Waddington (ed.) Univ. of Edinburgh Press.

R.Thom, A dynamical scheme for Vertebrate embryology, AMS Series on Math. Biology, 1973.

H.-O.WALTHER: Attraktivitätsbereiche von Funktionaldifferentialgleichungen für das Wachstum von Populationen

Das Populationsmodell (1) $\dot{n}(t) = [r - dn(t - \tau)] n(t)$ ist der Differenzen-Differentialgleichung (2) $\dot{x}(t) = -\alpha x(t-1) [1+x(t)]$ mit $\alpha > 0$ äquivalent. Dabei entspricht die Null-Lösung von (2) der konstanten Lösung von (1), und es ist $\alpha = r\tau$. Wir untersuchen in Abhängigkeit von α den Attraktivitätsbereich $A(\alpha)$ der Null-Lösung des Anfangswertproblems

(2') $x|_{[-1,0]} = \varphi$ ($\varphi: [-1,0] \rightarrow \mathbb{R}$ stetig vorgegeben),
 $x: [-1, \infty) \rightarrow \mathbb{R}$ ist stetig, x erfüllt (2) auf \mathbb{R}^+ ,

$A(\alpha)$ liegt stets in der Menge \tilde{C} aller Anfangsdaten φ mit $\varphi(0) > -1$. E.M.Wright bewies, daß die Null-Lösung für $\alpha < \frac{1}{2}$ asymptotisch stabil ist und daß für $\alpha \leq \frac{3}{2}$ $A(\alpha) = \tilde{C}$ gilt. - Ist $A(\alpha) = \tilde{C}$ für alle $\alpha \in (0, \frac{1}{2})$? Wir können zeigen, daß die Menge aller $\alpha \in (0, \frac{1}{2})$ mit $A(\alpha) = \tilde{C}$ offen ist. Anders gesagt: Der Attraktivitätsbereich \tilde{C} ist "stabil" gegen kleine Änderungen der Differenzen-Differentialgleichung. Ergebnisse dieses Typs erhalten wir auch für allgemeinere autonome retardierte Funktional-differentialgleichungen.

Erscheint in "manuscripta mathematica" 1975. E.M.Wright, A non-linear difference-differential equation, J. Reine Ang.Math. 194, 66-87(1955), J.Hale, Func.differential equations, Springer 1971, R.D.Nussbaum, A global bifurcation theorem with application to functional differential equations, to appear.

P.WALTMAN: Threshold induced delays in some epidemic and immunological models

The derivation of a model for the spread of an infection within a population will be described. The key point of the model is that a threshold condition is utilized which introduces a delay term into the equations. The existence of a positive solution is established and several numerical examples are provided. The same ideas are then applied in order to describe a model for the production of antibodies. Here there are two thresholds, one to account for the phenomenon of low dose tolerance and another to account for differentiation of the lymphocytes. Again, functional differential equations rather than ordinary ones arise as a result of the thresholds.

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H.WERNER: Ein Modell für die Reifung der roten Blutkörperchen

An der Universitätskinderklinik in Münster von Herrn Professor Schellong und seinen Mitarbeitern durchgeführte Versuchsreihen an Neugeborenen ergaben den zeitlichen Verlauf des Promillegehalts der roten Blutkörperchen an den verschiedenen Gruppen unreifer Teilchen (Retikulozyten) gemäß der Einteilung von Heilmeyer für die beiden ersten Wochen nach der Geburt. In diesem Zeitraum findet auch die Umstellung der Retikulozyten-erzeugung von der Leber auf das Knochenmark statt.

Aus den gemessenen Daten soll auf die Verweildauer in den einzelnen Gruppen und auf die Stärke der Produktion beider Quellen geschlossen werden. Zur Schätzung dieser Größen wird ein Verfahren beschrieben, das gewisse durch medizinische Fakten begründete Annahmen macht. Für die Dichte der Retikulozyten wird eine Differentialgleichung aufgestellt. Die gemessenen Werte sind die Integrale dieser Dichte über Intervalle, deren Größe zu schätzen ist. Das Verfahren kann auch bei anderen biologischen Messungen angewandt werden.

A. WÖRZ-BUSEKROS: Autosomale und geschlechtsgebundene Vererbung

Sowohl für den Fall von autosomaler als auch für den Fall von geschlechtsgebundener Vererbung bei Populationen mit getrennten Generationen und zufälliger Paarung werden Gameten- bzw. Zygoten-algebren definiert. Es werden hinreichende Bedingungen für die Existenz und Eindeutigkeit von nicht-trivialen Idempotenten in diesen Algebren angegeben. Für die Folgen der vollständigen Potenzen von Elementen mit Einheitsgewicht aus diesen Algebren werden Konvergenzkriterien angegeben. Bei geschlechtsgebundener Vererbung werden insbesondere die Fälle einfacher Mendel'scher Vererbung im weiblichen und im männlichen Geschlecht und der reine Mutationsfall untersucht.

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Gonshor, H., Special train algebras arising in genetics, Proc. Edinburgh Math.Soc. (2)12(1960), 41-53. Gonshor, H., Contributions to genetic algebras II, Proc. Edinb.Math.Soc.(2)18(1973),273-279, Wörz-Busekros, A., The zygotic algebra for sex-linkage, J. Math. Biology 1(1974), 37-46. Wörz-Busekros, A., The zygotic algebra for sex-linkage II, in Vorbereitung.

E.C. ZEEMAN: Gastrulation and formation of somites in amphibia and birds

A model, based on catastrophe theory consists of (1) the differentiation of mesoderm, causing a hidden primary wave (2) several hours later a resulting secondary wave of reduction of cell free-surface, causing changes of curvature and gastrulation, and (3) a resulting tertiary wave of increased cell adhesiveness, causing the formation of notochord. During the passage of the primary wave, mitosis forms a clock, interrupting development and causing the wave laterally to alternately move in spurts and pause. Therefore the resulting tertiary effect acts periodically on lateral mesoderm, thereby knocking off the somites. This model for somite formation avoids the standard difficulties of regulation suffered by classical gradient models. The same wave and clock model explains the similarities and differences between amphibian and bird embryos, and, in particular, explains the geometry of the primitive streak and Hensen's node.

E.C.Zeeman, Primary and secondary waves in developmental biology, Lectures in the Life Sciences, Vol. 7(1975), AMS Providence, USA.

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